

P. Swarajya LAKSHMI* & T. PULLAIAH*: **Studies on the
embryology of Anthemideae (Asteraceae)**

P.S. ラクシュミ*・T. プライア*: キク科キク連の胚学的研究

The tribe Anthemideae comprises 102 genera and approximately 1400 species (Heywood & Humphries 1978). Most embryological investigations of this tribe are confined only to the embryo sac development (see Pullaiah 1984). Information on anther and male gametophyte is available only in a few species, e.g. *Cotula australis* (Davis 1962), *Achillea squarrosa* (Pullaiah 1983) and others.

The present investigation includes the life histories of *Chrysanthemum indicum* Linn. and *Artemisia nitida* Willd. and some aspects of anther and ovule in *Santolina chamaecyparissus* Linn. Vernin (1952) studied the embryo development in *Chrysanthemum indicum* while Tateishi (1929) studied the embryo sac development in the same species. Chiarugi (1926a, b) reported the absence of fertilisation in *Artemisia nitida*.

Materials and methods The material of *Artemisia nitida* and *Santolina chamaecyparissus* was collected from Coonoor in Nilgiris in Tamilnadu and *Chrysanthemum indicum* from Anantapur town. Fixation was in formalin-acetic-alcohol (F.A.A). The usual methods of dehydration, infiltration, embedding and sectioning were followed. The sections were stained in Delafield's haematoxylin.

Observations Microsporangium, microsporogenesis and male gametophyte. In all the three investigated species there are four microsporangia in each anther (Figs. 1A, 3A). The male archesporium in the longitudinal section shows a single row of hypodermal cells (Fig. 5A). They divide periclinally to form a primary parietal layer towards outside and a primary sporogenous layer towards inside (Figs. 1B, 5B). The anther wall development corresponds to the Dicotyledonous type of Davis (1966) (Figs. 1C-E, 3E, 5C). The endothecium develops fibrous thickenings (Figs. 1G, 3F). The middle layer gets crushed and degenerated. The tapetal cells become binucleate (Figs. 1H, 5E). Later on nuclear divisions and fusions occur resulting in polyploid nuclei (Figs. 1I, 3G,

* Department of Botany, Sri Krishnadevaraya University, Anantapur 515003, A.P., India.

5H). In *Chrysanthemum indicum* at one-nucleate pollen grain stage the walls of the tapetal cells break down and the cytoplasm coalesce forming periplasmodium (Fig. 1F). It is used up by the developing pollen grains and no trace of it is left at maturity.

In *Artemisia nitida* the tapetal cells degenerate without forming a periplasmodium (Fig. 3D). Consequently, the pollen grains remain one-nucleate and become sterile. The tapetum formation in *Santolina chamaecyparissus* has not been studied.

The sporogenous cells in *Chrysanthemum indicum* and *Artemisia nitida* undergo divisions forming two rows of pollen mother cells (Figs. 1A, E, 3E), while in *Santolina chamaecyparissus* the sporogenous cells undergo only transverse divisions resulting in a single row of pollen mother cells (Fig. 5C). Pollen mother cells undergo meiotic divisions (Figs. 3J, K, 5G, H) resulting in microspore tetrads. Cytokinesis is of the simultaneous type (Figs. 1J, K, 5I, J). Microspore tetrads are either tetrahedral or decussate (Figs. 1L, 3L, M, 5K).

The microspores after their separation from the tetrad enlarge and acquire a thick exine (Figs. 1M, N, 3N, 5M, N). Further development has been studied only in *Chrysanthemum indicum* and *Artemisia nitida*.

In *Chrysanthemum indicum* the nucleus of the pollen grain divides to produce a generative cell and a vegetative cell. The generative cell moves into the vegetative cell (Fig. 1O). The pollen grains are 3-celled at shedding stage with three germ pores (Fig. 1P).

In *Artemisia nitida* the pollen grains remain one-nucleate even at the time of the dehiscence of anther. The cytoplasm in the pollen grains disintegrates and the pollen grains are sterile (Fig. 3D).

The exine in *Chrysanthemum indicum* (Fig. 1P) and *Santolina chamaecyparissus* (Fig. 5N) is echinate while in *Artemisia nitida* it is smooth (Fig. 3N, O).

Pollen grains which show signs of degeneration are also seen occasionally in *Chrysanthemum indicum*. Such pollen grains remain one-nucleate and devoid of any cytoplasmic contents (Fig. 1Q, R). In *Santolina chamaecyparissus* also microspores are found degenerating at microspore tetrad stage (Fig. 5L).

Ovary and ovule. The ovary is inferior, bicarpellary, syncarpous and unilocular with a single basal ovule. The ovule arises as a papillate growth from the base of the ovary but during subsequent development it curves and attains

anatropous condition during megasporogenesis (Figs. 2A-D, 3P, Q, 5O). The ovule is unitegmic and tenuinucellate. The cells of the inner epidermis of the integument during megaspore tetrad formation elongate radially, acquire dense cytoplasm and function as integumentary tapetum otherwise known as endothecium (Figs. 2G, 4B). It remains uniseriate with uninucleate cells throughout

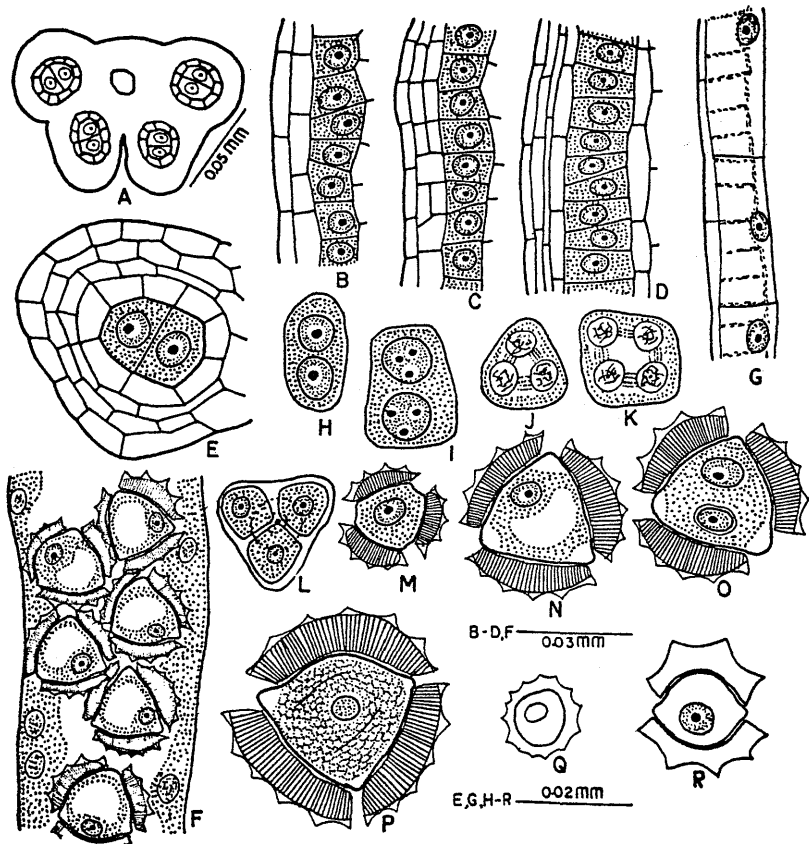


Fig. 1. *Chrysanthemum indicum*. A: Transverse section of anther at pollen mother cell stage. B-D: Longitudinal sections of part of anther lobe showing development of wall layers. E: Transverse section of anther lobe showing wall layers and pollen mother cells. F: Longitudinal section of part of anther lobe showing periplasmodium and one-nucleate pollen grains. G: Fibrous endothecium. H, I: Anther tapetal cells. J, K: Pollen mother cells in meiosis. L: Microspore tetrad. M, N: One-nucleate pollen grains. O: Two-celled pollen grain. P: Three-celled pollen grain. Q, R: Sterile pollen grains.

its further life.

Megasporogenesis and female gametophyte. The female archesporium is hypodermal and single-celled in *Chrysanthemum indicum* and *Artemisia nitida* (Fig. 2A, E), whereas in *Santolina chamaecyparissus* it is 6- to 8-celled (Fig. 5O-Q). Further development is studied only in *Chrysanthemum indicum* and

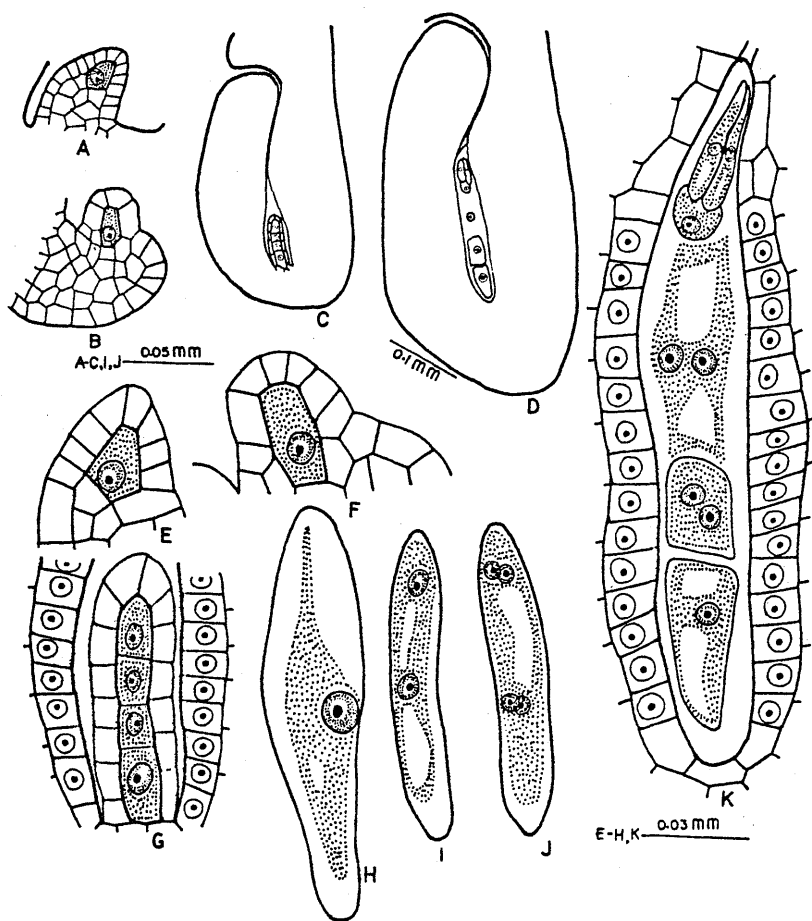


Fig. 2. *Chrysanthemum indicum*. A-D: Stages in the development of ovule. E: Female archesporial cell. F: Megaspore mother cell. G: Megaspore tetrad. H, I, J: One-, two- and four-nucleate embryo sacs respectively. K: Organized embryo sac.

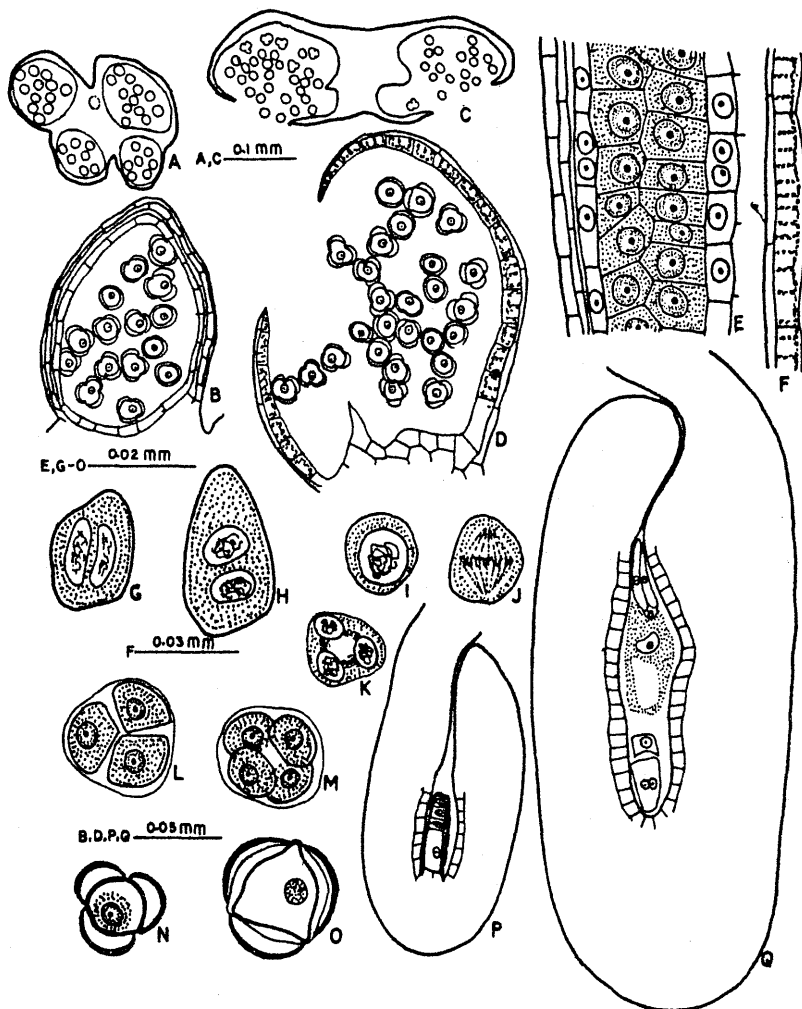


Fig. 3. *Artemisia nitida*. A: Transverse section of anther showing one-nucleate pollen grains. B: Portion enlarged from figure A. C: Transverse section of sterile anther showing one-nucleate pollen grains. D: Portion enlarged from figure C. E: Longitudinal section of part of another lobe showing wall layers and pollen mother cells. F: Fibrous endothecium. G, H: Anther tapetal cells. I-K: Pollen mother cells in meiosis. L, M: Microspore tetrads. N: One-nucleate pollen grain. O: Sterile pollen grain. P, Q: Ovules at tetrad and mature embryo sac stages.

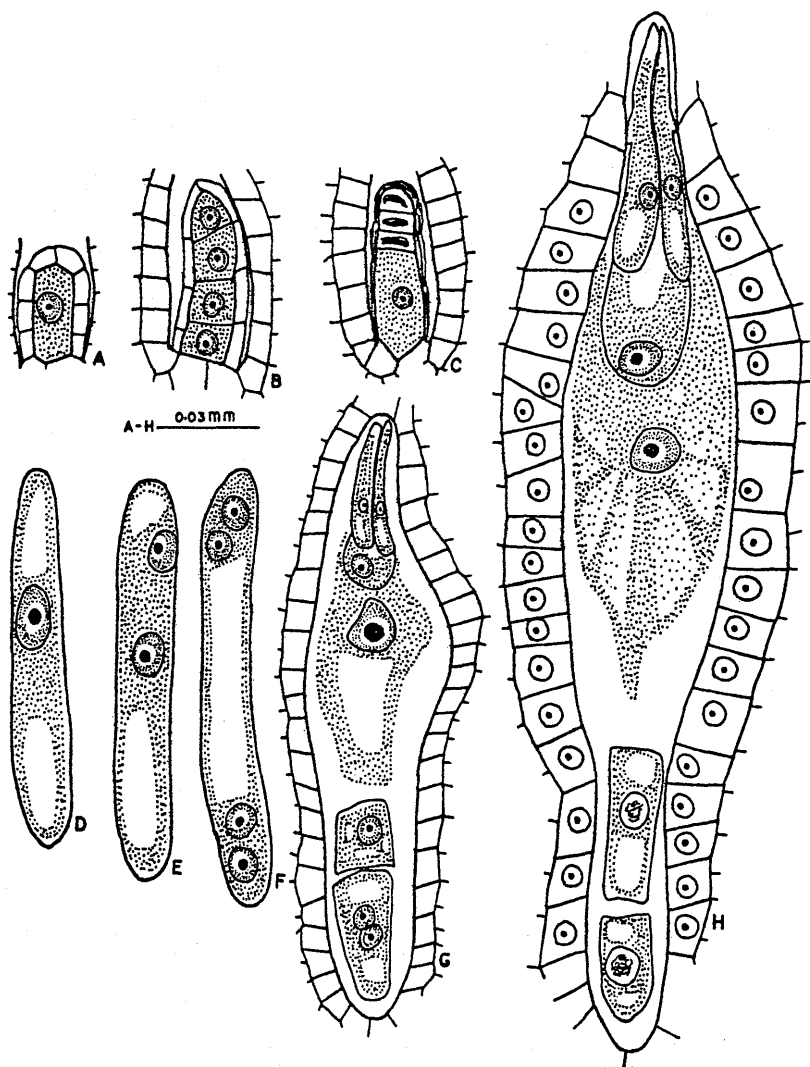


Fig. 4. *Artemisia nitida*. A: Megaspore mother cell. B: Megaspore tetrad. C: Megaspore tetrad with degenerating megaspores. D, E, F: One, two- and four-nucleate embryo sacs respectively. G, H: Young and mature embryo sacs respectively.

Artemisia nitida. The archesporial cell directly functions as megaspore mother cell (Figs. 2B, F, 4A) and enlarges considerably. A linear tetrad of megaspores is formed consequent upon the meiosis (Figs. 2G, 4B). The three microspylar megaspores degenerate while the chalazal megaspore enlarges and becomes functional (Fig. 4C). Its nucleus divides mitotically thrice to give rise to an 8-nucleate, 6-celled embryo sac of the *Polygonum* type (Figs. 2H-K, 4D-G). The synergids are hooked (Fig. 4H). The antipodal cells are two in number. In *Chrysanthemum indicum* the upper antipodal cell is binucleate (Fig. 2K) whereas in *Artemisia nitida* the lower cell contains two nuclei (Fig. 4G). The antipodals may become polyploid in *Artemisia nitida* due to nuclear divi-

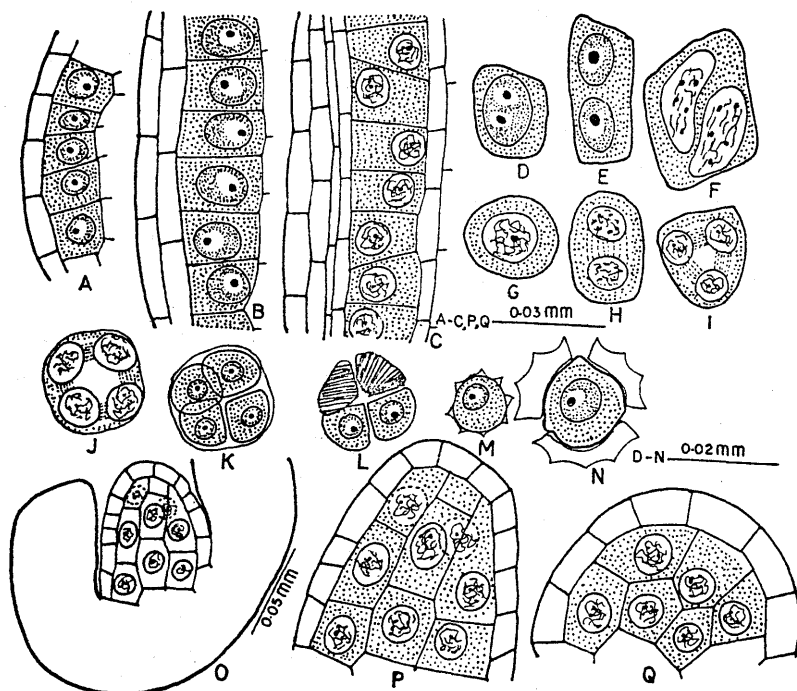


Fig. 5. *Santolina chamaecyparissus*. A: Longitudinal section of part of anther lobe showing archesporium. B: Longitudinal section of part of anther lobe showing one parietal layer and sporogenous layer. C: Longitudinal section of part of anther lobe showing wall layers and pollen mother cells. D-F: Tapetal cells. G-J: Pollen mother cells in meiosis. K: Microspore tetrad. L: Pollen tetrad with two degenerating microspores. M, N: Ore-nucleate pollen grains. O: Ovule showing multicelled archesporium. P, Q: Multicellular female archesporium.

sion and fusion (Fig. 4H). The two polar nuclei fuse resulting in the secondary nucleus which lies near the egg apparatus.

Fertilization, endosperm and embryo. As already mentioned, in *Artemisia nitida* the pollen grains are sterile and there is no fertilization and embryo and endosperm development. Propagation in this plant is vegetative only. In *Chrysanthemum indicum* also fertilization is absent. Consequently embryo and endosperm development is absent. Here also propagation is vegetative only.

Discussion In the development of anther wall, simultaneous cytokinesis, periplasmodial tapetum, 3-celled pollen grains and spinous exine the hitherto investigated members of the tribe Anthemideae—e.g., *Cotula australis* (Davis 1962), *Achillea squarrosa* (Pullaiah 1983) and *Chrysanthemum indicum* (present study)—show greater uniformity.

In *Artemisia nitida* (present study) the pollen grains are sterile due to the absence of periplasmodium formation.

Pollen degeneration is a frequent feature in *Chrysanthemum indicum* which was not reported hitherto in this tribe. Degeneration of microspores of a tetrad is also observed in *Santolina chamaecyparissus*.

A perusal of the available literature (see Pullaiah 1984) reveals that the occurrence of both uni- and multi-celled female archesporium is a common feature in this tribe. All the species of *Chrysanthemum* investigated so far showed multicelled archesporium except *C. viscidohirtum*, *C. arcticum*, *C. caucasicum*, *C. flosculosum*, *C. millefolium*, *C. camphoratum*, *C. vulgare* (Harling 1951), *C. viscosum* (Battaglia 1951), *C. ochroleucum* (Borgen 1972), and *C. indicum* (present study). The female archesporium in *Santolina chamaecyparissus* (present study) is multicelled as in some other members of the tribe.

The tribe Anthemideae is of great interest to the embryologists because of the occurrence of as many as three different types of embryo sac development viz., *Polygonum*, *Allium*, and *Drusa* type (Harling 1950, 1951, 1960, Borgen 1972). Besides these some unclassified types occur in plants like *Balsamita vulgaris* (Fagerlind 1930) and *Chrysanthemum cinerariaefolium* (Martinoli 1939). Harling (1951) reported three types of embryo sac development in different species of the genus *Chrysanthemum*. *C. indicum* (present study) shows *Polygonum* type of embryo sac development which is in conformity with Tateishi (1929). *Artemisia nitida* also shows *Polygonum* type of embryo sac development (present study) as in other species of the genus *Artemisia* (Weinedel-Liebau

1928). Chiarugi (1926a), however, observed in *Artemisia nitida* a multicelled female archesporium and unreduced embryo sacs as well as aposporic ones.

Vernin (1952) reported nuclear endosperm and Asterad type of embryogeny in *Chrysanthemum indicum*. But in our investigation fertilization and seed set was not observed. Throughout India this plant is propagated only vegetatively. Hence it is concluded that the plant investigated by Vernin (1952) may be another cytotype or a fertile variety. *Artemisia nitida* also does not show fertilization which is in conformity with the observation of Chiarugi (1926a, b) who also reported the absence of fertilization.

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キク科のキク連に属す *Chrysanthemum indicum* シマカンギクと, *Artemisia nitida* 及び *Santolina chamaecyparissus* (Lavender cotton) の胚学的研究を行った。*Artemisia nitida* の花粉形成は側壁層を形成せずに花粉は 1 核の状態で終り不稔であった。シマカンギクでは花粉は 3 細胞期まで進み花粉が形成された。両種とも胚嚢は正常に形成され共に *Polygonum* type である。しかし両種とも授精は行われず、胚乳も胚も形成されなかった。シマカンギクについては、胚乳形成は多核型で胚形成はコンギク型であるという報告があるが、その研究に使われた植物は核型が異なるか、稔性ある株なのであろう。本研究に使用したものは栄養繁殖の株のみである。

□CRC Handbook of lichenology Vols. I-III 625(297+181+147)pp. 1988. CRC Press, Florida. DM 798. 27名の地衣学者が、それぞれの専門の分野について執筆している。3巻からなる教科書である。第1巻では、地衣学研究史を含む序論から始まり、地衣体を構成する菌と藻および両者の相互の関係、生殖、炭素および窒素の代謝、酵素について述べている。第2巻では地衣類の colonization, 生長、生態および生態系における役割、共生体内で菌と藻がうける影響と地衣化がとり上げられている。第3巻では、二次代謝産物、貯蔵物質、色素、蛋白質などについて概説し、分類の原理、大気汚染との関連、地衣の有用性（利用と岩石の土壌化における役割）に及び、最後に地衣そのものの培養と分離した菌と藻の培養について略述している。最近の地衣学の発展は目覚ましく、3巻からなるこの教科書でも、十分に語りつくせるものではないが、全ての分野を概観するには適当であろう。ちょっと値段がはる（邦貨で約 80,000 円）のが難点である。

(黒川 道)